GENETIC ANALYSIS OF TEST DAY RECORDS OF MILK PRODUCTION IN DAIRY CATTLE

Opoku Baffour-Awuah

M. Phil.

University of Edinburgh

July, 1995

Abstract

Test day records of British Holstein-Friesian cows were considered as either multiple traits or repeated records in genetic analyses of performance of dairy cows in the second lactation. Estimates of genetic parameters of monthly test day and completed lactation records for milk, fat and protein yields were obtained using multivariate restricted maximum likelihood methods fitting a sire model. Generally, heritabilities for monthly test day yields were lower for early and later tests than for mid-lactation tests. The average estimates of correlation between adjacent test day records of all traits were 0.91 to 0.96 (genetic) and 0.56 to 0.71 (phenotypic). In general, the mean estimates decreased the further apart the test days. Estimates of genetic correlation of test day yields with corresponding lactation yields were highest (0.94 to 0.98) for mid-lactation records. The phenotypic correlations were lower than the corresponding genetic correlations, but both followed the same pattern.

Test day yields in the first three lactations were analysed using bivariate models to estimate genetic variance components for a trait between pairs of lactations. One year's records were considered in the analysis so that cows had records in only one lactation. The bivariate heritability estimates were generally lower than within lactation multivariate estimates for all traits. The heritability estimates were lower for test day yields at the beginning and the end of lactation than for test day yields taken in mid-lactation for all lactations. The heritability estimates for the complete lactation yields in lactations 1, 2 and 3 were all around 0.20 (ranging from 0.17 to 0.24) for milk, fat and protein yields. Genetic correlations between lactations 1 and 2 for test day yields taken in mid-lactation were higher

(0.92 – 0.95) than between lactations 1 and 3 (0.83 – 0.92) and between lactations 2 and 3 (0.81 – 0.89). Genetic correlations between lactations for test day records taken at the beginning and the end of lactation were, generally, low for all traits. Analysis of test day records was attempted assuming a repeatability model by considering all 10 individual test day records as repeated measurements of the same trait. The heritability estimates for milk, fat and protein yields were lower than the corresponding predicted estimates using average parameters from a multivariate model. Under a repeatability model, only a few test day records taken at mid-lactation may be considered most important with the intuitive assumption that heritabilities are equal for all the test day traits used and that the genetic correlation among all pairs of records is near unity.

Partial yields derived from test day yields were used to express the relative proportions of yield in three successive stages of lactation and to provide ratio measures for persistency of milk production. The ratio measures of persistency had moderate heritabilities and low genetic and negative phenotypic correlations with peak yield. The ratios based on partial variations in test day production were found to provide a good measure of persistency.

Acknowledgements

I would like to thank my supervisors, Professor Bill Hill and Dr Robin Thompson (Roslin Institute). I am grateful to the National Milk Records and Animal Data Centre for making the data available. I would also like to thank Dr Susan Brotherstone for offering computational assistance when needed. My heartfelt thanks to Dr Raphael Mrode of the Animal Data Centre for making useful comments at various stages of the study and also for his continuous encouragement and motivation.

Neither do I forget those friends and colleagues who helped me with my work, especially Mehmet Fırat of the Department of Mathematics and Statistics and those who shared an office with me for their useful comments and discussions.

Finally, my thanks go to the Ghana Government for funding my study and the University of Cape Coast, Ghana for granting me study leave; and to my wife, Felicia and children — Bernard, Eric and Lorraine and my entire family, both nucleus and extended, for their sustained love and moral support.

And to God be the glory!

Table of Contents

List of Tables

Chapter 1

General Introduction

1.1 Preamble

The genetic evaluation of lactation production in dairy cattle has, generally, been based on analysis of complete lactation (305-day) production. This is estimated from a set of test day yields, usually taken approximately at a monthly interval; and may often include predicted yields from information on partial lactations if completed yield information is unavailable for a lactation (Wiggans and Van Vleck, 1979; Weller, 1988). Normally, up to 10 – 12 test day measures are taken on cows to provide a complete lactation measure. It may be optimal to use test day yields directly for genetic evaluation instead of predicted yields for incomplete lactations. This avoids the problem of extending test day yields into a lactation record; and methods to combine test day yields into a single measure, especially for incomplete lactations, would not be necessary. By having six or more test day yields per cow per lactation, the accuracy of a cow's genetic evaluation may be better than having just a single record of the complete lactation yield. Similarly, dairy sires may be

more accurately proven by having a large number of test day yields available on their daughters rather than a single lactation record per daughter.

However, the use of test day yields in dairy cattle genetic evaluation has some potential limitations. Firstly, there is the need to store a large number of records of test day yields on individual cows instead of a single record based on 305-day yield. This inevitably would increase the computation time; hence the need to develop appropriate statistical models to handle and analyse test day records. Secondly, there is a strong dependence on the complete lactation yield for genetic evaluation of dairy cattle, and dairy cattle breeders need to be convinced about the use of a number of test day records in cow and sire evaluation in place of the traditional 305-day yield. Test day yields of milk production also provide a model for the study and analysis of quantitative traits with sequential repeated records.

1.2 Prediction of lactation production from test day yields

The desirability of utilizing all available information in dairy cattle genetic evaluation procedures has increased the importance of monthly test day records. In the broad sense, all models which incorporate records from single test days can be defined as test day models (Swalve, 1995). Part lactation records based on monthly test day records, therefore, appear to have an important position in dairy cattle breeding — both for bull and cow evaluation. Ptak and Schaeffer (1993) indicated that modelling individual test day yields can theoretically be more pre-

cise than modelling complete lactation yield for genetic evaluation. This is due to the fact that the linear interpolation of complete lactation yield from monthly test day yields has a phenotypic prediction error (predicted about the true yield) of about 2 to 3 per cent of the mean (Anderson, Mao and Gill, 1989). Projected (predicted) yields are thus often treated as having error variances greater than those of completed yields so that they will receive less emphasis in evaluations (Wiggans, Misztal and Van Vleck; 1988). VanRaden, Wiggans and Ernst (1991), however, indicated that projected yields actually have less variance than completed yields because coefficients of determination (i.e. squared correlations of predicted with true yield) are greater than 1.

The accuracy of prediction of breeding value for lactation yield from test day records depends on the number of test day yields and the genetic correlation of an index of test day yields with total lactation yield. The index of test day yields is, therefore, an important criterion. It is not clear how this index should be constituted based on either the number of monthly tests or any such combination of test day records. In forming an index, Keown and Van Vleck (1971) suggested that unequal weights to individual test days could be better than just adding the records. Meyer, Graser and Hammond (1989) found that correlations of 'canonical indices' which were linear functions of number of test records with lactation production were high, genetic correlations being essentially unity if five or more tests were considered, with heritabilities of test day milk traits being generally highest in the second trimester of lactation. Wilmink (1988) found that selection for second trimester yield is a useful alternative to selection for 305-day yield. Danell (1990) also indicated that test day yields in the mid-part of lactation had the

highest heritabilities and genetic correlations among themselves and with 305-day yields suggesting the scope for improvement of complete lactation yields by index selection incorporating test day records. If the optimum number of test yields to be recorded within a lactation on a cow for the prediction of complete lactation production is firmly established, then it may not be necessary to collect 10 or more test records per cow per lactation; and this could result in lower cost to dairy producers with very little loss in accuracy of genetic evaluation of dairy cattle. After six monthly test day records, additional monthly tests do not seem to warrant the effort and resources for collecting further milk test samples (Keown and Van Vleck, 1971; Ali and Schaeffer, 1987). Pander, Thompson and Hill (1993) indicated that less frequent than monthly testing (e.g. bi-monthly or 6-week intervals) would be sufficient for genetic evaluation of dairy cattle.

Studies conducted, so far, to examine the use of test day records for the genetic evaluation of dairy cattle have been limited to only the first lactation (Danell, 1982a; Meyer *et al.*, 1989; Pander, Hill and Thompson, 1992). Presently in the U.K., evaluation of dairy cattle is based on the first five lactations. However, using production records in the first two or three lactations, at least, may provide an accurate evaluation of lifetime performance (Meyer, 1984). Therefore, there is a need to obtain estimates of heritabilities of test day records and genetic correlations among test day records in multiple lactations; and on the basis of these parameters, determine an appropriate model for use of test day records in later lactations in genetic evaluation of dairy bulls and cows. There is, also, a need to find alternative selection criteria based on actual test day records during lactation or a linear function of test day records.

The analysis of test day records raises two fundamental issues regarding the accuracy to be gained by treating test day records as repeated records or as different but correlated traits. A repeatability model including successive test day records was recommended by Pander and Hill (1993) for predicting breeding value for heifer lactation records. Ptak and Schaeffer (1993) and Swalve (199%%ffffPrinterError:ffl a model which can be viewed as a repeatability animal model in which single test day records are taken as repeated measurements during lactation with factors in the model to account for the shape of the lactation curve. Due to the violation of the basic assumptions underlying the use of repeatability model, with regard to equal heritabilities across test days and genetic correlations of near unity between test day records for a trait (Danell, 1982a; Meyer *et al.*, 1989; Pander *et al.*, 1992), analyses of test day records as repeated measures may be considered multivariate. Against this background, the implications of using a repeatability model compared with a multi-trait model in the genetic analysis of traits like test day yields with repeated sequential records are not well studied (see Simianer, 1986; Van Vleck and Gregory, 1992).

1.3 Objective and Outline of Study

This study was an attempt to address some general problems associated with the analyses of test day yields of dairy cattle as traits with repeated sequential records. The objectives of the study were:

(i) to determine the appropriate statistical model for the genetic analysis of monthly

test day records when taken as different and correlated traits, and when considered as repeated records of the same trait;

(ii) to estimate genetic parameters for monthly test day records in multiple lactations using a bivariate model;

(iii) to establish the genetic relationship between partial yields derived from test day yields during different stages of lactation and persistency of milk production.

In Chapter 2, estimates of genetic parameters — heritabilities, genetic and phenotypic correlations — for individual monthly test day records of milk, fat and protein yields of British Holstein-Friesian cows in their second lactation obtained from a standard multi-trait analysis are reported. These records were independent of first lactation records used in an earlier study by Pander *et al.* (1992) in the same time frame. Genetic parameter estimation was carried out for test day yields in the first three lactations using bivariate analyses on similar test day yields taken in any two lactations. One year's records on daughters of the same sires were considered so that each cow had records in only one lactation. This special case of a bivariate model assumed that all residual covariances were zero as traits were measured on different animals at different times. The results of this analysis are presented in Chapter 3. In Chapter 4, estimates of variance components for test day yields in the second lactation under a repeatability animal model are reported; and the basic assumptions of a repeatability model and the implications of its use in the analysis of test day records are discussed. The results of a study on the genetic relationships between the partial milk yields representing yields in three successive stages of lactation derived from test day yields and persistency of milk

production are reported in Chapter 5. In Chapter 6, the general conclusions which are derived from these studies are highlighted.

Chapter 2

Analyses of test day records with a multivariate model

2.1 Introduction

If a number of test day records are measured on a cow in a lactation, then a general multivariate analysis with an appropriate model may be carried out, taking the individual records as different but correlated traits on a cow (Trus and Buttazzoni, 1990). One main advantage of multiple trait evaluation is that the accuracy of prediction is increased by the inclusion of more information about any particular trait and by improving the estimates of fixed effects through better connectedness of the data from creating more genetic links between sires and fixed effects. The potential benefits from a multivariate model for the genetic evaluation of farm livestock depends on the genetic and phenotypic variance and covariance structure of the traits considered (Thompson and Meyer, 1986). Therefore, if it is decided to use a multiple trait model for the genetic evaluation of farm livestock, accurate estimates of the correlation matrices between the traits are needed. The computational requirements of multi-trait analyses tend to be extensive. However, by

transforming to canonical scale, it is possible to reduce the evaluation to essentially separate univariate analyses when the data have the appropriate structure; i.e. if design matrices are equal and complete for all traits (Thompson, 1977; Meyer, 1985; Thompson and Hill, 1990).

The purpose of this study was to estimate heritabilities and genetic and phenotypic correlations between monthly test day records and complete lactation records. These estimates of genetic parameters would be useful in evaluating the efficiency of selection on the basis of individual test day records relative to complete lactation records. In addition, the importance of fitting different main fixed effects in the statistical model based on herd-month of first test or herd-season of first test to account for the environmental effects specific to the time of test was also examined.

2.2 Material and Methods

Multivariate analyses were carried out on test day records of British Holstein-Friesian cows between the ages of 32 and 60 months in their second lactation as a follow-up of previous study by Pander *et al.* (1992) on heifers from the same population. These records were considered separately as first lactation test day records were not available for these cows; and results may be affected by selection bias due to culling on the basis of first lactation performance (Nicholson, Schaeffer, Burnside and Freeman, 1978). One year's records taken in October, 1989 to September, 1990 were considered.

2.2.1 Data

The data used in the study consisted of test day records obtained by National Milk Records of the Milk Marketing Board of England and Wales on milk yield and of fat and protein contents of British Holstein-Friesian cattle in their second lactation. Variable intervals between test days instead of standardized intervals (i.e. 30-day intervals) were used. The interval between consecutive tests was kept between 20 and 50 days with the first test taken between 4 to 40 days after calving. The following conditions were set for a record to be included in the analyses:
(i) lactations shorter than 200 days and going beyond 440 days were ignored; and
(ii) interval between calvings was kept between 300 and 480 days.
These limits were set in order to delete outliers by subjective judgement based on histograms for these factors. For each test day, all records were required to be non-zero so that each cow had a complete information on all 10 test day measures taken for milk yield, fat and protein contents.

After these edits, 24345 records was extracted on cows from 6852 herds. These were records on daughters of 584 sires which were categorized as either random or proven (i.e. widely used) based on the year of birth of the bull in relation to his daughter's year of birth. Records on daughters of proven sires were included to improve the connectedness of the data but proven sires with fewer than 200 daughters were excluded from the data. The final data set comprised records on 19909 progeny of 35 proven bulls and 4436 progeny of 549 randomly used bulls. The number of daughters per proven sire varied between 232 and 1622 while the

corresponding figures for the randomly used sires were 5 and 28. About one-fifth of the data were on daughters of random sires.

Test day yields of fat and protein were calculated by multiplying test day milk yield by fat and protein contents. The complete lactation yields (based on 305-day production) of milk, fat and protein were computed from test day yields using the standard linear interpolation method according to the Milk Marketing Board's Method 3 formula (British Standards Institution; 1972):

$$LY = (I_1 \times TY_1) + (\sum_{n=1}^{9} I_{n+1} \times (TY_n + TY_{n+1})/2) + (I_{10} \times TY_{10}) \qquad (2.1)$$

where:

LY = complete lactation yield of milk, fat and protein;

TY = test day yield of milk, fat and protein(1 to 10);

I_{n+1} = interval between TD_n and TD_{n+1} where $n = 1, \ldots, 9$;

I_1 = days in milk at first test;

I_{10} = lactation length - days in milk to TD_{10}, if lactation length is less than 305 days; or

I_{10} = 305 - days in milk to TD_{10}, if lactation length is greater or equal to 305 days.

The lactation fat and protein contents were calculated by dividing the lactation fat and protein yields by lactation milk yield. Test day and complete lactation records on milk, fat and protein yields were the traits analysed. All cows had records for all traits.

2.2.2 Statistical Models and Analyses

Preliminary univariate analyses were carried out for each test day record and the complete lactation record for milk, fat and protein yield separately. In subsequent multivariate analyses, all 10 test day records and the complete lactation record for a particular trait were considered simultaneously. Three main fixed effects considered in the partitioning of the environmental variation were (i) herd-year-season of first test (HYST); (ii) herd-year-month of first test (HYMT) and (iii) herd and month of first test as cross-classified effects but ignoring their interaction. These gave three different models used in the analyses. The effect of season of first test considered in Model 1 was accounted for by classifying season of first test into six 2-monthly classes from October to September. For the one year's production cycle, October 1989 was taken as Month 1 and September 1990 as Month 12.

In all the three models, additional fixed effects considered were the pedigree status of cows and widely used (proven) sires. In Model 3, month of first test was considered as an additional fixed effect. For the univariate analyses of individual test day records taken at a specific time in the lactation, days in milk at each test, i.e. interval from calving to respective test was taken into account by fitting it as a covariate. For the analyses of lactation yields of milk, fat and protein, lactation length was considered instead of days in milk at test. The multivariate analyses involved all the test day records for a particular milk trait simultaneously; and days in milk to the first test was the covariable considered. The other effects fitted as covariates in all models for both analyses were age at calving and the proportion of Holstein in sires to account for nonadditive breed effects.

For the genetic analysis of test day and complete lactation records, a restricted maximum likelihood procedure (Patterson and Thompson, 1971) was followed using REMLPK programs (Meyer, 1986) fitting a sire model. In order to minimize any bias due to selection of sires, proven sires were considered as fixed effects so that their daughters' records did not contribute to the between-sire variance component (Van Vleck, 1985). Therefore, only the variance between young sires was utilized to estimate the additive genetic variance. This assumed that residual variances were homogeneous for daughters of both types of sires. The covariance among the young sires due to the genetic relationship between them through their sires (i.e. paternal grandsires of the cows) was taken into account by incorporating a relationship matrix between the random sires.

The univariate mixed linear model used was of the general form:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zs} + \mathbf{e} \tag{2.2}$$

where

$\mathbf{y}$ = vector of observations;

$\mathbf{X}$ = incidence (design) matrix for fixed effects and covariables;

$\mathbf{Z}$ = incidence (design) matrix for sire effects;

$\mathbf{b}$ = vector containing all fixed effects and covariables;

$\mathbf{s}$ = vector of sire effects;

$\mathbf{e}$ = vector of random residual errors.

Because sire effects were considered both as fixed for the proven sires and as random for the young sires, the design matrix for the sire effects may be partitioned into two components as:

$$\mathbf{Z} = \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{bmatrix} \tag{2.3}$$

Also the vector of sire effects can be partitioned as:

$$\mathbf{s} = \begin{bmatrix} \mathbf{s}_1 \\ \mathbf{s}_2 \end{bmatrix} \tag{2.4}$$

where $\mathbf{Z}_1$ and $\mathbf{Z}_2$ are the design matrices for fixed sire and random sire effects respectively; $\mathbf{s}_1$ and $\mathbf{s}_2$ are the vectors of fixed and random sires effects respectively.

For this model, it was assumed that

$E(\mathbf{y}) = \mathbf{Xb} + \mathbf{Z}_1\mathbf{s}_1$ and $E(\mathbf{s}_2) = \mathbf{0}$; $E(\mathbf{e}) = \mathbf{0}$.

Furthermore, $var(\mathbf{s}_2) = \mathbf{A}_s\sigma^2{}_s$ and $var(\mathbf{e}) = \mathbf{I}\sigma^2{}_e$. Also $cov(\mathbf{s}_2, \mathbf{e}) = \mathbf{0}$ where $\mathbf{A}_s$ = additive relationship matrix of random sire effects; $\mathbf{I}$ = identity matrix; $\sigma^2{}_s$ = sire component of variance and $\sigma^2{}_e$ = residual component of variance.

The multivariate model is a direct extension of the univariate model (2.2) when the design matrices are equal for all traits (Meyer, 1985). The univariate analyses carried out provided estimates of variance components and heritability for each test day and 305-day lactation milk, fat and protein yields. From the variance-covariance components for test day and 305-day milk, fat and protein yields obtained by the multivariate analyses, heritabilities of the traits and genetic correlations among them were estimated.

Genetic variances or covariances were calculated as four times the estimated between-sire components. Phenotypic variances and covariances were the sum of estimated between- and within-sire (residual) variance or covariance components.

2.3 Results

2.3.1 Characteristics of fixed effect models

The characteristics of Models 1, 2 and 3 fitting different main effects are shown in Table 2–1. For Model 1, a total of 14108 HYST subclasses were generated from the available records with 61.7% having one record per subclass and 77.0% with only one sire per subclass. For Model 2, there were 16142 HYMT subclasses from the available records with 69.8% of the subclasses having only one record and 82.6% with one sire per subclass. Model 3 had 29.0% of subclasses with single record and 47.4% with one sire per subclass. Another feature of the models was the average number of effective records per sire due to different number of contemporaries within each main effect subclass. Model 2 had the smallest average number of effective records per sire, 1.90 compared with 2.30 for Model 1 and 3.93 for Model 3. As the number of subclasses increases, the number of sires with effective records decreases.

The maximum proportions of the total sums of squares for all the test day yields of milk, fat and protein explained by the different main fixed effects fitted

Table 2–1: Characteristics of Models 1–3 fitting different main fixed effects.

	MODEL 1	MODEL 2	MODEL 3
Main fixed effect	HYST	HYMT	HERD
No. of subclasses	14108	16142	6852
Av. No. of records/subclass	1.72	1.51	3.55
Total No. of effective records	984.08	774.18	1849.24
No. of sires with effective records	427	408	470
Av. No. of effective records/sire	2.30	1.90	3.93
% Subclass with one record	61.7	69.8	29.0
% Subclass with one sire	77.0	82.6	47.4

Table 2–2: Maximum proportions (%) of the total sums of squares for all the test day yields of milk, fat and protein accounted for by the different main fixed effects fitted in Models 1–3 and the degrees of freedom for residual.

	MODEL 1	MODEL 2	MODEL 3
Test day milk yields	76	82	58
Test day fat yields	79	83	61
Test day protein yields	79	83	62
Degrees of freedom for residual	9612	7578	16857

in the models used are shown in Table 2–2. Also given are the degrees of freedom for residual after fitting the main fixed effects for Models 1, 2 and 3.

2.3.2 Phenotypic means of individual test day records

Overall phenotypic means, standard deviations and coefficients of variation for days in milk at each test and different traits of test day and complete lactation records are given in Table 2–3.

On average the first test was taken at 18 days after calving with subsequent tests taken at an average interval of 30–31 days. The average test day yields of milk, fat and protein decreased as lactation progressed. The decline in production was more acute from test day 8 onwards for all traits. The standard deviations of test day yields of milk, fat and protein showed much variability during early lactation with coefficients of variation increasing steadily during the second half of lactation. The fat content of milk was higher than the protein content for all the test day and lactation records. Both fat and protein contents increased as lactation progressed.

2.3.3 Genetic parameter estimates

Estimates of sire and residual variance components and heritability for the individual test day and lactation yields of milk, fat and protein obtained from models fitting the different main fixed effects are summarised in Tables 2–4 to 2–6 for multivariate analyses. Model 2 gave higher estimates of heritability for all the traits.

Table 2–3: Phenotypic means, standard deviations (SD) and coefficient of variation (CV) for days in milk at test and different traits of test day (TD) and complete lactation (LAC) records. (No. of records = 24345).

	TD1	TD2	TD3	TD4	TD5	TD6	TD7	TD8	TD9	TD10	LAC
Days in milk at test†											
Mean	18	48	78	109	139	170	200	230	260	291	
SD	8.91	9.05	9.15	9.20	9.13	9.11	9.13	9.11	9.14	9.14	
CV(%)	50.0	18.8	11.7	8.4	6.6	5.4	4.6	3.9	3.5	3.1	
Milk yield(kg)											
Mean	25.5	26.0	24.1	22.2	20.5	19.1	17.9	16.6	14.7	11.8	6078.5
SD	5.10	5.18	5.01	4.77	4.60	4.47	4.38	4.25	4.15	4.31	1113.4
CV(%)	20.1	19.9	20.8	21.5	22.4	23.4	24.4	25.6	28.3	36.6	18.3
Fat yield(kg)											
Mean	1.022	0.985	0.931	0.875	0.826	0.784	0.740	0.690	0.624	0.525	244.4
SD	0.248	0.230	0.216	0.203	0.191	0.185	0.181	0.179	0.178	0.188	45.77
CV(%)	24.3	23.3	23.3	23.2	23.2	23.6	24.5	25.9	28.5	35.8	18.7
Protein yield(kg)											
Mean	0.849	0.806	0.763	0.715	0.669	0.629	0.600	0.569	0.520	0.436	200.2
SD	0.169	0.161	0.159	0.154	0.148	0.146	0.145	0.144	0.142	0.149	34.69
CV(%)	19.7	19.8	20.7	21.3	21.9	23.0	24.1	25.1	27.2	34.1	17.3
Fat Content(g/kg)											
Mean	40.2	38.0	38.8	39.7	40.5	41.3	41.6	41.9	42.9	45.2	40.4
SD	6.02	5.55	5.73	5.80	5.77	5.92	5.95	5.98	6.19	6.95	3.97
CV(%)	15.5	14.6	14.8	14.6	14.2	14.3	14.3	14.3	14.5	15.4	9.8
Protein Content(g/kg)											
Mean	33.5	31.1	31.7	32.4	32.7	33.6	33.5	34.4	35.7	37.5	33.0
SD	3.64	2.53	2.66	2.70	2.65	2.59	2.58	2.62	2.88	3.68	1.94
CV(%)	10.8	8.1	8.4	8.3	8.1	7.9	7.7	7.6	8.1	9.8	5.9

† Interval from calving to test.

Table 2–4: Estimates of sire (σ_s^2) and residual (σ_e^2) variance components for test day (kg^2) and complete lactation ($kg^2 \times 10^3$) milk yields and their corresponding heritability estimates with standard errors from multivariate analyses.

MODEL 1: fitting HYST

	TD1	TD2	TD3	TD4	TD5	TD6	TD7	TD8	TD9	TD10	LAC
σ_s^2	0.63	1.03	1.08	1.11	1.68	1.54	1.13	1.46	1.26	1.14	93.46
σ_e^2	13.99	13.44	12.76	12.15	11.54	11.22	11.59	11.51	11.96	13.56	621.55
h^2	0.17	0.28	0.31	0.34	0.51	0.48	0.36	0.45	0.38	0.31	0.52
s.e.	0.056	0.105	0.080	0.088	0.113	0.105	0.082	0.107	0.104	0.091	0.114

MODEL 2: fitting HYMT

	TD1	TD2	TD3	TD4	TD5	TD6	TD7	TD8	TD9	TD10	LAC
σ_s^2	0.93	1.48	1.25	1.30	2.14	1.55	1.48	1.59	1.39	1.02	104.07
σ_e^2	13.85	13.11	12.65	11.96	11.33	11.09	11.29	11.36	11.74	13.45	617.11
h^2	0.25	0.41	0.36	0.39	0.64	0.49	0.46	0.49	0.42	0.28	0.58
s.e	0.078	0.119	0.094	0.095	0.141	0.118	0.114	0.129	0.112	0.103	0.128

MODEL 3: fitting HERD + MONTH

	TD1	TD2	TD3	TD4	TD5	TD6	TD7	TD8	TD9	TD10	LAC
σ_s^2	0.69	1.13	1.30	1.33	1.59	1.32	1.05	1.39	1.16	0.82	89.83
σ_e^2	14.91	14.43	13.57	12.73	12.31	12.01	12.18	12.47	12.65	14.42	654.47
h^2	0.18	0.29	0.35	0.38	0.46	0.40	0.32	0.40	0.34	0.22	0.48
s.e	0.055	0.067	0.070	0.071	0.077	0.071	0.060	0.076	0.067	0.063	0.082

Table 2–5: Estimates of sire (σ_s^2) and residual (σ_e^2) variance components for test day ($kg^2 \times 10^{-3}$) and complete lactation fat yields ($kg^2 \times 10$) and their corresponding heritability estimates with standard errors from multivariate analyses.

MODEL 1: fitting HYST

	TD1	TD2	TD3	TD4	TD5	TD6	TD7	TD8	TD9	TD10	LAC
σ_s^2	1.54	2.40	1.98	1.46	2.05	2.18	2.08	3.17	2.72	2.91	17.18
σ_e^2	35.86	29.71	26.89	24.45	21.48	20.26	21.17	21.66	22.66	26.20	100.37
h^2	0.16	0.30	0.27	0.23	0.35	0.39	0.36	0.51	0.43	0.40	0.58
s.e.	0.087	0.085	0.072	0.075	0.095	0.096	0.092	0.112	0.095	0.109	0.119

MODEL 2: fitting HYMT

	TD1	TD2	TD3	TD4	TD5	TD6	TD7	TD8	TD9	TD10	LAC
σ_s^2	1.86	2.44	2.05	1.90	2.59	2.53	2.90	3.42	3.36	2.86	20.46
σ_e^2	34.88	29.54	26.98	24.08	21.10	20.37	21.02	21.48	22.38	26.16	100.02
h^2	0.21	0.30	0.28	0.29	0.44	0.44	0.49	0.55	0.52	0.39	0.68
s.e	0.128	0.098	0.080	0.088	0.139	0.107	0.124	0.131	0.124	0.120	0.141

MODEL 3: fitting HERD + MONTH

	TD1	TD2	TD3	TD4	TD5	TD6	TD7	TD8	TD9	TD10	LAC
σ_s^2	1.06	1.50	2.00	1.51	1.69	1.64	1.58	2.37	1.88	1.85	12.49
σ_e^2	38.73	31.44	28.41	25.23	22.44	21.64	22.01	22.95	23.67	27.65	105.40
h^2	0.11	0.18	0.26	0.23	0.28	0.28	0.27	0.38	0.29	0.25	0.42
s.e	0.040	0.052	0.062	0.056	0.066	0.064	0.064	0.072	0.057	0.063	0.079

Table 2–6: Estimates of sire (σ_s^2) and residual (σ_e^2) variance components for test day ($kg^2 \times 10^{-3}$) and complete lactation protein yields ($kg^2 \times 10$) and their corresponding heritability estimates with standard errors from multivariate analyses.

MODEL 1: fitting HYST

	TD1	TD2	TD3	TD4	TD5	TD6	TD7	TD8	TD9	TD10	LAC
σ_s^2	0.61	0.88	0.53	0.54	0.85	1.23	1.13	1.67	1.24	1.19	7.37
σ_e^2	15.21	11.90	11.87	11.55	11.23	11.27	12.31	12.65	13.72	16.08	56.15
h^2	0.15	0.28	0.17	0.18	0.28	0.39	0.34	0.47	0.33	0.27	0.46
s.e.	0.069	0.100	0.065	0.050	0.080	0.096	0.087	0.111	0.095	0.091	0.112

MODEL 2: fitting HYMT

	TD1	TD2	TD3	TD4	TD5	TD6	TD7	TD8	TD9	TD10	LAC
σ_s^2	1.04	1.03	0.55	0.78	1.22	1.43	1.57	1.73	1.43	0.94	8.86
σ_e^2	15.12	11.73	11.78	11.35	10.95	11.04	11.86	12.42	13.47	16.00	55.82
h^2	0.26	0.32	0.18	0.26	0.40	0.46	0.47	0.49	0.38	0.22	0.55
s.e	0.083	0.108	0.060	0.070	0.103	0.109	0.111	0.131	0.110	0.094	0.127

MODEL 3: fitting HERD + MONTH

	TD1	TD2	TD3	TD4	TD5	TD6	TD7	TD8	TD9	TD10	LAC
σ_s^2	0.58	0.83	0.88	0.96	1.18	0.95	0.95	1.36	1.08	0.93	7.12
σ_e^2	16.52	13.22	12.90	12.44	12.21	12.41	13.20	13.99	14.55	16.98	59.32
h^2	0.13	0.24	0.26	0.29	0.35	0.28	0.27	0.35	0.27	0.21	0.43
s.e	0.044	0.056	0.061	0.058	0.072	0.061	0.062	0.073	0.060	0.055	0.079

However, the heritability estimates obtained from Model 2 had higher standard errors when compared with those of the estimates from the other models. This is due to the small average number of effective records per sire. Model 3 gave low estimates of heritability for all traits but with low standard errors. The heritability estimates and standard errors for all traits obtained from Model 1 were between those obtained from Models 2 and 3. For all the models used, the residual variance was higher at the beginning and towards the end of lactation than in mid-lactation.

For all the traits, the heritability of test day 1 was lowest but the heritability of test day yield increased steadily as the number of test day records advanced being highest in mid-lactation and declining towards the end of lactation. Generally, the heritability estimates of milk traits based on single test day records were high during the second-half of lactation. In all cases the heritabilities for the individual test day yields were lower than for the corresponding complete lactation yield. The heritability estimates for fat yield were higher than those for milk and protein yields. The heritability estimates for lactation records were higher for milk and protein yields than for fat yield.

Details of estimates of heritability, genetic and phenotypic correlations among test day and lactation yields of milk, fat and protein are given in Tables 2–7 to 2–9 as the full correlation matrices obtained from the multivariate analyses under Model 1. From these correlation matrices the mean genetic and phenotypic correlations among test day records as a function of number of test apart were calculated as follows: for example, the mean correlation among test day records 3

Table 2–7: Estimates of heritability (×100) (diagonal), genetic (below diagonal) and phenotypic (above diagonal) correlations (×100) among test day (TD) and complete lactation milk yield (LMY). Estimates from Model 1 fitting HYST.

	TD1	TD2	TD3	TD4	TD5	TD6	TD7	TD8	TD9	TD10	LMY
TD1	**17**	60	53	47	43	39	33	29	21	12	59
TD2	93	**28**	68	63	58	53	46	39	30	20	72
TD3	83	89	**31**	71	66	62	55	49	39	27	79
TD4	76	83	99	**34**	74	68	61	55	45	31	82
TD5	73	80	98	99	**51**	76	67	59	50	35	84
TD6	67	68	93	96	98	**48**	73	64	54	38	83
TD7	61	57	85	90	92	98	**36**	70	60	44	80
TD8	61	45	73	77	79	90	94	**45**	72	57	78
TD9	59	43	66	70	73	83	91	93	**38**	72	71
TD10	48	40	57	60	62	73	82	89	98	**31**	58
LMY	80	77	94	96	96	98	96	89	87	80	**52**

Range of s.e.(h^2) = 0.06 to 0.11. Range of s.e.(r_p) = 0.006 to 0.017.

Range of s.e.(r_g) = 0.003 for r_g = 0.99 to 0.192 for r_g = 0.40.

Table 2–8: Estimates of heritability (×100) (diagonal), genetic (below diagonal) and phenotypic (above diagonal) correlations (×100) among test day (TD) and complete lactation fat yield (LFY). Estimates from Model 1 fitting HYST.

	TD1	TD2	TD3	TD4	TD5	TD6	TD7	TD8	TD9	TD10	LFY
TD1	**16**	37	34	29	28	25	23	19	16	10	51
TD2	72	**30**	44	41	38	36	32	30	25	17	60
TD3	76	91	**27**	48	45	44	42	38	32	24	67
TD4	60	92	88	**23**	54	51	46	44	38	30	70
TD5	52	70	74	88	**35**	60	55	51	46	37	74
TD6	50	77	78	91	99	**39**	62	57	52	44	77
TD7	61	70	79	82	96	97	**36**	63	59	48	76
TD8	58	64	60	83	97	97	90	**51**	66	56	75
TD9	50	70	68	83	96	97	95	97	**43**	66	72
TD10	42	52	51	66	87	88	89	91	96	**40**	61
LFY	74	83	95	92	96	98	97	91	96	86	**58**

Range of s.e.(h^2) = 0.07 to 0.12. Range of s.e.(r_p) = 0.006 to 0.016.

Range of s.e.(r_g) = 0.019 for r_g = 0.99 to 0.227 for r_g = 0.42.

Table 2–9: Estimates of heritability (×100) (diagonal), genetic (below diagonal) and phenotypic (above diagonal) correlations (×100) among test day (TD) and complete lactation protein yield (LPY). Estimates from Model 1 fitting HYST.

	TD1	TD2	TD3	TD4	TD5	TD6	TD7	TD8	TD9	TD10	LPY
TD1	**15**	49	43	38	35	30	27	26	21	15	55
TD2	88	**28**	56	51	47	41	37	33	27	21	65
TD3	81	85	**17**	60	54	50	44	42	35	28	71
TD4	78	74	98	**18**	63	57	49	48	41	32	75
TD5	74	80	98	98	**28**	65	55	51	44	36	77
TD6	61	62	93	97	96	**39**	63	56	47	36	76
TD7	56	50	86	94	91	98	**34**	62	53	40	75
TD8	55	48	87	93	88	95	95	**47**	65	53	76
TD9	70	42	74	85	72	80	85	86	**33**	67	71
TD10	55	50	79	86	73	78	81	87	98	**27**	62
LPY	80	72	96	99	96	96	94	93	89	90	**46**

Range of s.e.(h^2) = 0.06 to 0.13. Range of s.e.(r_p) = 0.004 to 0.016.

Range of s.e.(r_g) = 0.005 for r_g = 0.99 to 0.202 for r_g = 0.42.

tests apart was calculated as the average of correlations between test days 1 and 4, 2 and 5, 3 and 6, 4 and 7, 5 and 8, 6 and 9, and 7 and 10; and for test day records 8 tests apart as the average between test days 1 and 9, and 2 and 10. The results are shown in Table 2–10.

The mean genetic correlations were higher than the mean phenotypic correlations. In general, the estimates of both genetic and phenotypic correlations declined the further apart the test days; and normally, test day records that are close together are more highly correlated than records that are further apart for the same trait. Genetic and phenotypic correlations between test days and lactation yields of milk, fat and protein are presented in Table 2–11 for Model 1. Genetic correlations between test day and lactation records for all traits were high from test day 3 onwards with the highest estimates occurring at mid-lactation between test day 4 and test day 7. Test days 1 and 2 records were poorly correlated to lactation records. Phenotypic correlations followed a similar pattern but were lower than genetic correlations.

The heritability estimates of lactation yields of milk, fat and protein are given in Table 2–12 from univariate and multivariate analyses under Model 1. For the univariate analysis and the first multivariate analysis, the effect of lactation length was accounted for as a covariable; while in the second multivariate analysis, the days in milk to first test was considered as a covariable. The multivariate analyses gave similar estimates for the same lactation yield traits which is an indication that fitting lactation length as a covariable had the same effect as days in milk to first test.

Table 2–10: Average genetic (r_g) and phenotypic (r_p) correlations ($\times 100$) among test day milk, fat and protein yields as a function of number of tests apart (T_a). Estimates from Model 1 fitting HYST.

	Milk Yield		Fat Yield		Protein Yield	
T_a	r_g	r_p	r_g	r_p	r_g	r_p
1	92	71	91	56	93	61
2	90	62	89	50	89	53
3	83	55	82	44	85	46
4	75	49	79	40	78	41
5	66	43	70	34	71	37
6	58	36	65	29	66	32
7	54	29	60	23	59	27
8	50	21	51	17	60	21
9	48	12	42	10	55	15

Table 2–11: Genetic (r_g) and phenotypic (r_p) correlations ($\times 100$) of test day records with complete lactation records for milk, fat and protein yields. Estimates from Model 1 fitting HYST.

	Lactation Record					
	Milk Yield		Fat Yield		Protein Yield	
Test day	r_g	r_p	r_g	r_p	r_g	r_p
1	80	59	74	51	80	55
2	77	72	83	60	72	65
3	94	79	95	67	96	71
4	96	82	92	70	99	75
5	96	84	96	74	96	77
6	98	83	98	77	96	76
7	96	80	97	76	94	75
8	89	78	91	75	93	76
9	87	71	88	72	89	71
10	80	58	86	61	90	62

Table 2–12: Heritabilities† of lactation yields of milk, fat and protein.

	Univariate	Multivariate I	Multivariate II
LMY	0.49	0.50	0.52
s.e.	0.13	0.12	0.11
LFY	0.54	0.55	0.56
s.e.	0.12	0.12	0.12
LPY	0.45	0.46	0.46
s.e.	0.12	0.12	0.11

† Estimates from univariate and multivariate analyses under Model 1 fitting HYST. In the univariate and the first multivariate analyses, lactation length was fitted as a covariable; and in the second multivariate analysis, the covariable considered was the interval between calving and first test.

2.4 Discussion

The main fixed effects fitted in the three models tested gave different subclass numbers and proportions with one record and one sire per subclass. For any given model, the main effect subclasses with only one record contribute information on other fixed effects in the model while those with one sire would contribute information only to the residual (within-sire) variance. Reducing subclass size resulted in an increased number of sires without effective records. Consequently estimates of sire components varied between models.

The different main fixed effects accounted for varying proportions of the total sums of squares (TSS) for the different traits. In general, fitting only the herd effect as the main fixed effect (Model 3) explained a much lower proportion of variation while the herd-year-month of first test effect accounted for a much higher proportion of variation. Therefore, fitting this effect (Model 2) reduced residual variances in all traits over estimates from Models 1 and 3, showing the importance of accounting for environmental effects specific to time of test. Herd-year-month of calving or herd-year-season of calving has been found to be more appropriate for lactation traits (Chauhan and Hill, 1986). However, for the analysis of test day records, a fixed effect common to all test day records of all cows taken in a particular herd-year-month of first test is expected to reduce the overall residual variance of test day yields considerably (Meyer *et al.*, 1989; Pander *et al.*, 1992), and thus, likely to be more important than herd-year-season of calving. It is generally known that ignoring certain fixed effects actually present in the model leads to biased es-

timators. The mean square error is sometimes used as a measure of accuracy of a model (Henderson, 1975b). High heritability estimates were obtained for all traits using Model 2 due to a relatively increased sire and reduced residual components of variance and also because HYMT accounted for a greater proportion of TSS for all traits compared to the other main fixed effects fitted in the other models. The differences in the estimates of heritability and their standard errors obtained from the different models of analysis are due to the differences in the magnitude of the between- and within-sire variance components and the average number of effective records. The heritability estimates and their standard errors for all traits obtained under Model 1, fitting herd-year-season of first test, were between those obtained under Models 2 and 3. Model 1 was therefore adopted for the analyses to provide estimates of genetic parameters for all the traits.

Generally, the multivariate estimates of heritability were slightly higher than estimates obtained from the univariate analysis of the same trait. Although the models used in the two analyses were different only with respect to days in milk to test fitted as a covariable, a multiple trait model utilizes available information (correlations among traits) and thereby gives more accurate evaluations than a single trait model due to an improved data structure under a multivariate analysis. The potential benefits from a multivariate evaluation also relate to the genetic and phenotypic variance and covariance structure of the traits considered (Thompson and Meyer, 1986).

Results obtained from the analysis of second lactation records for the estimates of heritabilities of test day records and correlations between them were consistent

with the results for first lactation test day records reported by Pander *et al.* (1992). In this study, the second lactation records were considered independent of first lactation records. Therefore, any culling on the basis of first lactation production had not been accounted for. The small effects of selection bias in sire evaluation for second lactation records as reported by various workers (e.g. Wickham and Henderson, 1977; Nicholson *et al.*, 1978; Eriksson, 1982; Cassell and McDaniel, 1983; Strandberg, 1990) indicated that the problem was not too serious and could be ignored. However, the heritability estimates of test day records obtained in the current study were higher than those reported for other dairy cattle populations in their first lactation (e.g. Danell, 1982a; Meyer *et al.*, 1989). But the pattern for genetic parameters of test day records in the present study for cows in their second lactation was similar to other published reports, with a general trend toward an increasing heritabilities for all traits in mid-lactation. The heritability estimates of test day records taken during the early part of lactation were generally low due to both a relatively high within-sire component and a low between-sire component of variance.

The heritability estimates for lactation yields from both univariate and multivariate analyses were higher for second lactation than estimates obtained from previous analyses on British Friesian and Friesian-Holstein cattle (e.g. Barker and Robertson, 1966; Meyer, 1984; Visscher and Thompson, 1992). The reason for this may be due to their use of inappropriate models for the analysis of lactation performance. Most published reports on genetic parameters of lactation performance are based on a herd-year-season model which usually yields lower heritability estimates due to a relatively increased within-sire and reduced between-sire components of

variance compared with the variance components obtained under a test day model with herd-month of first test as the main fixed effect. Another possible reason is the presence of non-additive effects in crossbred populations which may bias the heritability upwards (Van der Werf and De Boer, 1989). At the time cows in the data were born, the U.K. population of Holstein-Friesian was becoming more crossbred due to the rapid introduction of North American Holstein genes with the mean proportions of Holstein genes in the bulls and cows being 0.42 and 0.34 respectively with many $F1s$ around (S. Brotherstone, personal communication). In the current analysis, the proportion of Holstein in the sires was accounted for as a covariable. Pander *et al.* (1992) adopted this and other strategies to account for the non-additive effects, but these had little effect on the heritability estimates in heifers.

The estimates of parameters from multivariate analysis could be employed in the genetic evaluation of dairy cattle regarding individual test days as different traits. If computing facilities are not limiting, these estimates and those obtained by Pander *et al.* (1992) for the first lactation records may be combined in a multiple lactations genetic evaluation of test day records. In practice, this is not feasible; for such a multivariate analysis of test day records in multiple lactations will involve up to about 20 test day yields for a yield trait in first and second lactations. On the other hand, the estimates of genetic parameters could be used in developing a phenotypic index as described by Pander and Hill (1993) for the prediction of 305-day lactation yield for second lactation from test day yields. The predicted 305-day yield would be used for genetic evaluation to develop appropriate weights depending on the number of test days. This will result in daughters of

bulls being evaluated early on the basis of the second lactation test day records in place of 305-day yield for a complete lactation record and hence reduce the time to obtain reliable proofs for bulls. Reduction of time for evaluation means reduction in generation interval and therefore faster genetic progress. The parameters from the multivariate analysis provide a good framework for further investigation on how to model individual test day records in genetic evaluation of dairy cattle.

Chapter 3

Bivariate analysis of test day yields in multiple lactations

3.1 Introduction

Analysing test day records in multiple lactations using a multivariate model may not be computationally feasible due to the number of parameters involved. In the circumstance, within lactation multivariate model may seem appropriate. However, selection bias is likely to affect the estimates of genetic parameters and components of variance. In particular, variances estimated for second lactation production are bound to be biased if culling is based on performance in the first lactation (Henderson, 1990). This may be avoided by considering test day records in a later lactation from cows for which similar test day records are present in the previous lactation. Another option is to carry out a series of bivariate analyses on similar test day records taken on different animals in any two lactations. Computationally, this bivariate model ignores the covariance among errors to estimate genetic variance and covariance components for a test day trait in any two lactations simultaneously using the procedure suggested by Schaeffer, Wilton and

Thompson (1978). This procedure involved considering yields of different cows in two lactations as separate traits with zero error covariances between them. For the analysis of test day yields of cows in multiple lactations, it is expected that some repeated records on the same cow occur in different lactations. In such situations, some covariances between error terms on the same animal might be expected. An alternative approach might be the use of the procedure presented by Rothschild, Henderson and Quaas (1979) by which error covariances are derived from cows with records in two or more lactations. However, this is computationally more complex than the one used by Schaeffer *et al.* (1978). Otherwise, traits in any two lactations may be analysed separately ignoring the existence of a non-zero component of covariance under a basically univariate model.

In this study, test day yields in the first three lactations were analysed using a bivariate model to estimate genetic variance components for a trait between pairs of lactations. One year's records were considered in the analyses so that cows had records in only one lactation; therefore yields in any two lactations were considered as different traits measured on different cows with all residual covariances being zero.

3.2 Material and Methods

3.2.1 Data

Records on 32928, 27534 and 21271 daughters of 162 sires in lactations 1, 2 and 3 respectively were extracted from National Milk Records of the Milk Marketing Board of England and Wales for test day records taken from October, 1989 to September, 1990. These were different cows each with records in only one lactation. To improve the data structure, records of daughters of the most widely sires with at least 20 progeny in each lactation were used. The following limits were set for records included in the data set:

(i) the first test was taken between 4 and 40 days after calving with the interval between consecutive tests kept from 20 to 50 days; and

(ii) interval between calvings was kept between 300 and 480 days.

Each cow in the data set had complete information on 10 test day measures of milk, fat and protein yields but only test days 1, 5 and 10 taken at the beginning, middle and end of lactation in addition to the complete lactation yields were the traits considered in the analyses.

3.2.2 Statistical Model and Analyses

Bivariate analyses were carried out on pairwise combinations of a given trait in different lactations to estimate variance components. The approach used was a restricted maximum likelihood estimation procedure for data with one random

effect for a special case where the same traits are measured on different animals in different environments so that all residual covariances are zero, based on a computational strategy described by Schaeffer *et al.* (1978).

The general mixed model for a bivariate analysis used was of the form:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{s}_1 \\ \mathbf{s}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} \tag{3.1}$$

where

$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix}$ = a vector of observations for a trait in any two lactations;

$\begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix}$ = a vector of all fixed effects and covariables for traits 1 and 2;

$\begin{bmatrix} \mathbf{s}_1 \\ \mathbf{s}_2 \end{bmatrix}$ = a vector of sire effects for traits 1 and 2;

$\begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix}$ = a vector of residuals for traits 1 and 2.

$\mathbf{X}_1$, $\mathbf{X}_2$ and $\mathbf{Z}_1$, $\mathbf{Z}_2$ are incidence matrices for fixed effects and covariables and for random effects respectively for traits 1 and 2. The design structures for these matrices were different for any given trait in two lactations.

The sire effects were assumed to have mean zero and variance-covariance matrix of the form:

$$var \begin{bmatrix} \mathbf{s}_1 \\ \mathbf{s}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{I}\sigma^2_{s1} & \mathbf{I}\sigma_{s1s2} \\ \mathbf{I}\sigma_{s1s2} & \mathbf{I}\sigma^2_{s2} \end{bmatrix}$$

where $\mathbf{I}$ is identity matrix, σ^2_{s1} and σ^2_{s2} were sire variance components for a trait in any two lactations and σ_{s1s2} the covariance between them.

The residuals were also assumed to have mean zero and variance matrix of the form:

$$var \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{I}\sigma^2_{e1} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}\sigma^2_{e2} \end{bmatrix}$$

where σ^2_{e1} and σ^2_{e2} were variance components within sires for a trait in any two lactations. All residual covariances are zero. Furthermore, the covariance between the random effects was assumed to be zero; i.e. $cov(\mathbf{s}, \mathbf{e}) = \mathbf{0}$.

In these analyses, the main fixed effect fitted was herd-year-season of first test with the season of first test made up of two consecutive months of first test within lactation as considered in Model 1 for the multivariate analysis of second lactation records reported in Chapter 2. The pedigree status of cows was considered as the additional fixed effect. The proportion of Holstein in the sire, age at calving and days in milk to test for the test day records or lactation length for the complete lactation records were fitted as covariables. In these data sets, all sires, including those with large number of daughters and therefore selected, were treated as random. Including records of daughters of widely used and selected bulls provides more comparisons between lactations and within main effects but treating effects of such sires as random would bias estimates of sire component

of variance. Genetic variances and covariances were estimated as four times the between-sire components. For this analysis sires were assumed to be unrelated. Test day records for all pairwise combinations of lactations 1, 2 and 3 for each trait (i.e. as lactations 1 and 2, 2 and 3, 1 and 3) were considered simultaneously and analysed as separate traits on different cows under a bivariate model.

3.3 Results

The characteristics and summary statistics of the data sets used in the bivariate analyses are presented in Table 3–1.

The heritability estimates obtained for each trait from the bivariate analyses of each pair of lactations were not different for each lactation. Therefore, each pair of estimates was averaged to give a single estimate for each trait in each lactation. For example, the heritability estimates for milk yield for TD 1 in lactation 1 obtained from the bivariate analysis of lactations 1 and 2, was not much different from that obtained from the bivariate analysis of lactations 1 and 3 ; and the heritability estimate for milk yield for TD 1 in lactation 1 was obtained as a pooled estimate (simple average) of the two estimates. These and the genetic correlations between the pair of lactations for each trait are given in Table 3–2.

Generally, heritability estimates for test days 1 and 10 yields were lower than test day 5 yields. Genetic correlations between lactations for the test day 5 records were high, and for lactations 1 and 2 were close to unity for all traits. Genetic correlations between lactations 1 and 3 for test days 1 and 10 yields were found to

Table 3–1: Characteristics and summary statistics of data sets for bivariate analyses.

Lactation	1	2	3
Number of records	32928	27534	21271
No. of HYST subclasses	14634	13848	12322
Mean age at calving (months)	30.6	42.5	54.9
Traits			
Mean milk yields (kg)			
TD1	19.60	25.61	28.20
TD5	17.70	20.72	22.81
TD10	12.92	11.88	11.99
Lactation	5313.3	6125.1	6655.9
Mean fat yields (kg)			
TD1	0.796	1.026	1.141
TD5	0.717	0.830	0.899
TD10	0.572	0.528	0.527
Lactation	215.47	245.68	264.35
Mean protein yields (kg)			
TD1	0.637	0.852	926
TD5	0.576	0.673	731
TD10	0.460	0.438	0.441
Lactation	173.02	201.28	215.75

Table 3–2: Bivariate estimates of heritability (pooled h^2) of test day and lactation yields in lactations 1, 2 and 3 and genetic correlations (r_g) between lactations for each trait.

Trait	h_1^2	h_2^2	h_3^2	r_{g12}	s.e.	r_{g13}	s.e.	r_{g23}	s.e.
Milk yield									
TD1	0.13	0.16	0.11	0.86	0.066	0.58	0.135	0.75	0.107
TD5	0.20	0.15	0.18	0.95	0.041	0.92	0.055	0.87	0.072
TD10	0.12	0.16	0.18	0.78	0.083	0.48	0.138	0.78	0.093
Lactation	0.22	0.23	0.23	0.87	0.051	0.84	0.065	0.84	0.065
Fat yield									
TD1	0.12	0.11	0.10	0.94	0.058	0.67	0.128	0.82	0.106
TD5	0.11	0.12	0.15	0.92	0.063	0.83	0.088	0.81	0.095
TD10	0.09	0.15	0.15	0.76	0.095	0.39	0.155	0.73	0.101
Lactation	0.17	0.23	0.24	0.86	0.058	0.79	0.076	0.80	0.072
Protein yield									
TD1	0.08	0.12	0.09	0.89	0.075	0.59	0.154	0.76	0.122
TD5	0.14	0.11	0.15	0.99	0.042	0.90	0.070	0.89	0.079
TD10	0.11	0.13	0.14	0.71	0.103	0.47	0.142	0.73	0.112
Lactation	0.21	0.20	0.24	0.87	0.054	0.82	0.067	0.85	0.064

be generally lower (0.39 – 0.67) than the genetic correlations between lactations 1 and 2 (0.71 – 0.94), and lactations 2 and 3 (0.73 – 0.82) for all traits. In general, genetic correlations between adjacent lactations (r_{12} and r_{23}) were higher than between non-adjacent lactations (r_{13}) for all the test day yields.

The heritability estimates for the complete lactation yields in lactations 1, 2 and 3 were 0.22, 0.23 and 0.23 for milk, 0.17, 0.23 and 0.24 for fat and 0.21, 0.20 and 0.24 for protein respectively. The genetic correlations between lactations for any trait were slightly higher for lactations 1 and 2 and lactations 2 and 3 than for lactations 1 and 3. For the adjacent lactations, the genetic correlations for all traits ranged between 0.80 to 0.87 while the genetic correlation between non-adjacent lactations for all traits was between 0.79 to 0.84.

3.4 Discussion

The purpose of using a bivariate analysis to estimate the variance and covariance components of milk traits is usually to adjust for bias due to selection in the previous lactation. In particular, variance components estimated for traits in lactations 2 and 3 will be biased if culling was based on performance in the first lactation. Should this happen, heritabilities of later lactations and correlations between lactations are expected to be biased downwards. However, the procedure used in these bivariate analyses did not account for selection since traits in any two lactations were measured on different cows and not as repeated records on the same cow. The bivariate estimates of genetic parameters for test day yields

were lower than the multivariate estimates obtained for second lactation records in previous analyses (Chapter 2) and those reported for first lactation records by Pander *et al.* (1992). The main reason for the lower bivariate estimates of heritability obtained in this study for test day yields seems to be due to the fact that all sires were considered random in the model of analysis. Because the data used in the analysis included records on daughters of proven bulls, genetic parameter estimates might have been reduced because of selection. As proven bulls contributed to the estimation of sire components, all heritabilities were expected to underestimate the true values (Van Vleck, 1985; Meyer, 1987). Considering the most widely used bulls as fixed would eliminate the bias due to such selection (Henderson, 1975a), but the inclusion of records on daughters of the most widely used sires improved the data structure across lactations. In the analysis, sires were also assumed unrelated; and in ignoring the relationship among sires, the effect of inbreeding was not accounted for in the estimation of genetic parameters. Inbreeding can directly cause a decrease in genetic variation and this might have affected the result of the analysis.

For the complete lactation yields, the heritability estimates obtained in these analyses, though biased downwards, were similar to those reported in the review by Maijala and Hanna (1974) and references therein and those reported for later studies by Tong, Kennedy and Moxley (1979), Meyer (1984) and Simianer (1986) for milk and fat yields in the first three lactations (Table 3–3). However, these estimates were lower than those obtained for similar traits by Visscher and Thompson (1992) in pedigree cows and those within lactation estimates for first lactation obtained by Pander *et al.* (1992) and for second lactation reported in Chapter 2. The

Table 3–3: Summary of literature estimates of heritability for lactation milk and fat yields in the first three lactations.

	Milk Yield			Fat Yield		
Author(s)	h_1^2	h_2^2	h_3^2	h_1^2	h_2^2	h_3^2
Maijala & Hanna (1974)	0.26	0.20	0.17	0.25	0.16	0.17
Tong *et al.* (1979)	0.26	0.19	0.17	0.26	0.17	0.15
Meyer (1984)	0.28	0.20	0.24	0.27	0.21	0.25
Simianer (1986)	0.23	0.21	0.24	0.23	0.25	0.23
Visscher & Thompson (1992)	0.40	0.33	0.30	0.37	0.31	0.29
Present study	0.22	0.23	0.23	0.17	0.23	0.24

main reasons for the high estimates obtained by Visscher and Thompson (1992) seem to be due to the fact that heritability estimates from pedigree populations are often higher than from non-pedigree or mixed populations due to preferential treatment of pedigree herds which gives rise to higher variances between sires (Meyer, 1987). Further, animal model-REML estimates are a combination of estimates from daughter-dam regression and from paternal half-sib correlation and, therefore, tend to be high. In all these studies, genetic correlations between lactations for milk traits were greater than 0.80 and, in most cases, close to unity. These were similar to those obtained in this study, especially for test day 5 and lactation yields. The estimates obtained for both test day yields and completed lactation yields confirmed that genetic correlations for milk traits between adjacent lactations tend to be higher than between non-adjacent lactations (Tong *et al.*, 1979).

In genetic evaluation of dairy cattle in multiple lactations, genetic correlations between lactations of unity is, usually assumed, notably under a repeatability model, implying that different lactations are genetically the same trait and sires would rank the same independent of lactation number (Tong *et al.*, 1979). The high genetic correlations between adjacent lactations for mid-lactation test day yields indicated that mid-lactation test day yields in the first three lactations could be regarded as the same traits. On the other hand, the generally low genetic correlations between first and third lactations for test days 1 and 10 yields was an indication that different genes influence performance at the different lactations for these particular test days at the beginning and toward the end of lactation. The low genetic correlations between the first and third lactations for test day

yields for test days 1 and 10 could also indicate a change in sire rankings with age and parity of cows for these traits. Lee (1978) proposed methods of evaluating dairy sires for milk yield based on records which are adjusted for effects of age at calving and eliminating effects of sire and herd-year-seasons. Sire evaluation with yield ignoring age at calving would be appropriate only when the correlations of yield with age at calving due to sires are zero. Wickham and Henderson (1977) suggested the use of an appropriate age factor as a fixed effect to remove lactation effects in order to explain the changes in performance in different lactations. In this analysis, age at calving considered as a covariate seemed not to have removed the effects due to lactation which explained the differences in test day yields at the beginning and towards the end of lactation. However, it is not clear how records should be adjusted for effects of age at calving since measurements in the different lactations were taken on different animals.

Chapter 4

Analysis of test day records with a repeatability model

4.1 Introduction

Recently, interest has been shown in the use of test day models as a replacement of evaluations of dairy cattle based on 305-day production. Ptak and Schaeffer (1993) suggested a test day model which can be explained as a repeatability animal model considering single test day records as repeated measurements and accounting for the shape of lactation by means of regression factors. Essentially, the repeatability model looks at multiple recordings of test day yields as repetitions of one trait. With the repeatability model, a random permanent environmental effect is included to account for environmental correlations between test day measurements within a lactation. The repeatability model for analysing test day records may thus explain both permanent environmental effects affecting individual cows across all test days and temporal environmental effects specific to a particular cow concerning the general condition of a cow on a given test day; for example whether a cow is ill, pregnant or in a special management group or feeding regime

within a herd. The inclusion of this additional random effect allows for the general condition of a cow on a specific test day to be accounted for.

Basically, a repeatability model for analysing test day records assumes equal heritabilities across test days and genetic correlation of unity between test days. Another assumption is that the environmental correlations are the same for all pairs of records. These assumptions are often violated as indicated by results from multivariate analyses of test day records (e.g. Meyer *et al.*, 1989; Pander *et al.*, 1992). In these studies, heritabilities of test day yields within lactation were generally found to be lower during early and late lactations than in mid-lactation. Also both genetic and phenotypic correlations between any two test day records reduced the further apart the test days with test days that were close together being more highly correlated than records that were further apart. See also the results from multivariate analysis presented in Chapter 2.

Despite these limitations of using a repeatability model in the genetic analysis of test day records, the prediction of breeding values for lactation records from test day records assuming a repeatability model is simpler computationally, and seems to be suitable alternative to a multivariate model (Pander and Hill, 1993). In most countries where all available lactation records are utilized in the genetic evaluation of dairy cattle, a repeatability model is used with little or no loss in efficiency (Wiggans *et al.*, 1988; Jones and Goddard, 1990). There are no estimates of genetic parameters for test day yields applying a repeatability model. This analysis was carried out to estimate variance components for test day yields of milk, fat and protein for cows under a repeatability animal model; and based

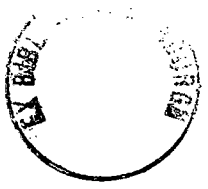
on the magnitudes of these estimates assess the suitability of using a repeatability model for the analysis of test day records.

4.2 Material and Methods

4.2.1 Data

Records on British Holstein-Friesian cows in their second lactation were extracted from the National Milk Records of the Milk Marketing Board for cows calving from October, 1989 to September, 1990. This was similar to the data set used for previous analyses of test day records with a multivariate model. The main fixed effect considered was herd-year-season of test which was an effect common to all test day yields of cows taken over a two-month period in the same herds. The number of the main fixed effect levels from the available records was too large to be accomodated due to limits in computing facilities. Therefore, herd-year-season of test classes with less than 2 records were deleted. This resulted in the final data set based on 4319 herd-year-season of test classes. These were records on 5314 cows each with a complete set of 10 test day records for yield of milk, fat and protein giving 53140 records for each trait. The cows were daughters of 655 sires.

4.2.2 Statistical Models and Analyses



In the analyses, the pedigree status of cows was considered as the additional fixed effect; and days in milk for a test day yield, which indicated the stage of lactation

when a particular test day record was taken, and the age at calving in months were both fitted as quadratic covariates. All animal effects, including those of proven sires, were treated as random. The effect of permanent environment of a cow on each test day was considered as a second random effect. Theoretically, addition of the components of variance due to both random effects will give an estimate of the covariance between phenotypic records on the same animal.

The following test day repeatability model (Swalve, 1993) was used:

$$y_{ijkl} = HYS_i + ps_j + bX + a_k + pe_k + e_{ijkl} \tag{4.1}$$

where:

y_{ijkl} = a single test day record for milk, fat or protein yield;

HYS_i = effect of herd-year-season of test;

ps_j = effect of pedigree status of cows;

b = linear and quadratic regression coefficients;

X = covariates of age at calving and days in milk to specific test;

a_k = random cow's additive genetic effect;

pe_k = random effect of permanent environment of the cow at each test day;

e_{ijkl}= random error (residual) effect.

Variance components were estimated using DFREML programs (Meyer, 1991) applying univariate animal models with genetic relationships among cows included. The second random effect due to permanent environment was estimated as the c^2 - term (i.e. common environmental effect). In the analysis, the covariance structure for the second random effect was assumed to be proportional to the identity matrix and uncorrelated to the direct additive genetic effect due to each cow.

The analysis of repeated records, for example test day yields in cows, follows the general repeatability model (Van Vleck and Gregory, 1992):

$$y_{ij} = \mu + g_{ij} + e_{ij} \tag{4.2}$$

with $i = 1, ..., b$ for the number of cows; and $j = 1, ..., n$ for the number of observations per cow; where y_{ij} is the j^{th} test day record on cow i, g_{ij} is the genetic value for the j^{th} record on cow i, and e_{ij} the environmental effect on the j^{th} record on cow i.

Under a repeatability model, it is assumed that heritability for each record is equal and environmental and genetic covariances between all possible pairs of records on the same cow are equal. Therefore:

$V(e_{ij}) = \sigma_e^2$ and $V(g_{ij}) = \sigma_g^2$

$cov(e_{ij}, e_{ij'}) = \sigma_{ee'}$ and $cov(g_{ij}, g_{ij'}) = \sigma_{gg'}$ for $j \neq j'$.

This model is equivalent to the usual repeated-records model when $\sigma_{gg'} = \sigma_g^2$ where: $r_g = \sigma_{gg'}/\sigma_g^2 = 1$ (i.e. a genetic correlation of unity between records); and $r_e = \sigma_{ee'}/\sigma_e^2$. The usual repeatability model thus assumes $r_g = 1$ and a common environmental covariance among pairs of measures.

Van Vleck and Gregory (1992) indicated that the average genetic correlation multiplied by the average heritability from a multiple-trait model, $(r_g h^2)_M$, may be a good prediction of heritability from a repeated-records model, h_R^2, assuming equal heritabilities and phenotypic correlations and genetic correlation of unity. With this model, the phenotypic correlations between pairs of test day records are

$$(r_g\sigma_g^2 + r_e\sigma_e^2)/(\sigma_g^2 + \sigma_e^2) \tag{4.3}$$

for both the repeatability model(R) and multi-trait model(M). Thus, if $(r_g h^2)_M$ is used to predict h^2_R, then $(r_p)_M - (r_g h^2)_M$ could be used to predict the permanent environmental effects, the c^2-term in a repeated-record model, where $(r_p)_M$ is the average phenotypic correlation from the multi-trait model. These predictors from a multi-trait model assume equal heritabilities and phenotypic correlation and genetic correlation of unity with environmental correlation of nearly zero.

The estimates of heritability and permanent environmental effect from a repeatability model were thus predicted from the average correlation and heritability estimates obtained from multi-trait model as $(r_g h^2)_M$ and $(r_p)_M - (r_g h^2)_M$ respectively.

4.3 Results

The complete record based on 10 successive test day yields of milk, fat and protein and the estimates of variance components of test day yields under a repeatability model are shown in Table 4–1. For a repeatability model, a complete record for the yield each of milk, fat and protein was assumed to be the mean phenotype of 10 successive records of test day yields. These were similar to the phenotypic mean yields for test day 5 taken at mid-lactation. See Table 2–3 of Chapter 2.

Table 4–1: Mean yield (kg) and estimates of variance components† (kg^2), heritability (h^2), repeatability (t) and permanent environmental effect ($p.e.$) for test day milk, fat and protein yields.

Trait	Mean	S.D.	σ^2_A	σ^2_E	σ^2_{PE}	h^2	$s.e$	$p.e$	$s.e$	t
Milk	20.060	6.446	2.563	6.803	4.402	0.19	0.037	0.32	0.034	0.51
Fat	0.806	0.252	3.78	1.63	6.95	0.14	0.031	0.26	0.028	0.40
Protein	0.668	0.198	1.98	7.67	4.27	0.14	0.031	0.31	0.028	0.45

† Additive (A), residual (E) and permanent environment (PE) variance components for fat and protein yields ($\times 10^{-3}$).

The estimates of the permanent environmental effect, c^2 were 0.32, 0.26 and 0.31 for milk yield, fat yield and protein yield respectively. The heritability estimates for the test day yields under the repeatability model were 0.19, 0.14 and 0.14 with repeatability estimates of 0.51, 0.40 and 0.45 for milk, fat and protein yields respectively. The estimates of heritability for milk, fat and protein yields predicted from average correlations and heritabilities from the multi-trait model were 0.27, 0.25 and 0.23. The corresponding predicted estimates of permanent environmental effect were 0.24, 0.16 and 0.21 for milk, fat and protein yields respectively (Table 4–2). Compared with the actual estimates of the permanent environmental effect under a repeatability model, the predicted estimates were similar for milk and fat yields but lower for protein yield. The estimates of permanent environmental

Table 4–2: Predicted estimates of heritability (h_R^2) and permanent environmental effect (*p.e.*) for repeatability model compared with estimates from multivariate analyses for test day milk, fat and protein yields.

	Average multivariate estimates†			Predicted estimates	
Trait	$(r_g)_M$	$(r_p)_M$	h_M^2	h_R^2	*p.e.*
Milk	0.77	0.51	0.36	0.27	0.24
Fat	0.75	0.41	0.34	0.25	0.16
Protein	0.79	0.44	0.29	0.23	0.21

† Average of 10 test day records per trait.

effect and repeatability obtained from this study were consistent with estimates from complete lactation records reported by Visscher and Thompson (1992).

4.4 Discussion

For each trait, the heritability estimate obtained under a repeatability model was lower than the predicted estimate from the average heritabilities obtained for the multi-trait model. Since the analysis of test day records using a repeatability model was based on a subset of cows used in the multivariate analysis, the lower heritability estimates obtained might be due to sampling. However, the main reason seems to be the violation of the assumptions for the usual repeatability model. When the assumptions for a repeatability model are wrong the consequences may be that parameters are underestimated (Van Vleck and Gregory, 1992). The assumptions violated in this study were those implied in a repeated-records animal model, namely, the genetic correlation between consecutive records is unity, the phenotypic correlations are the same for all pairs of records, and heritabilities are equal for all records.

In a simulation study of ovulation rate, Van Vleck and Gregory (1992) found that even in the situation where the assumptions behind the repeatability model were violated, the multivariate estimates could be used to predict the heritability and the fraction of variance due to permanent environmental effects in the repeated-records model. Although there were no obvious patterns in the genetic and environmental correlations, the genetic and permanent enviromental variances

added together to estimate the covariance between the phenotypic records on the same animal. In this study, data sets on ovulation rate with multivariate, binomially distributed variables were transformed to multivariate, normal variables. It was concluded by Van Vleck and Gregory (1992) that in situations where genetic and environmental covariances among repeated records are not equal for all pairs of records, the expectations of the genetic and permanent environmental variances depend on the covariance pattern. For test day records, the covariance structure shows a well-defined pattern with test day records that are close together being more highly correlated than records that are further apart for the same trait (see Chapter 2). This suggests that a repeatability model may not be appropriate for analysing test day records of milk production in dairy cattle as repeated records.

Most repeatability models are based on few multiple records because the gain in accuracy declines rapidly as the number of records increases, and it may not be worthwhile to use more than two or three repeated records (Falconer, 1989). The current U.K. national genetic evaluation of dairy cattle uses up to five lactation records assuming a repeatability model (Animal Data Centre, 1995). Under this model, all records are assumed to have equal genetic variance and the repeatability model may be incorrect without the necessary adjustments to account for unequal variances (VanRaden *et al.*, 1991; Pander and Hill, 1993). For the analysis of test day yields under a repeatability model, the inclusion of more records (up to 10 as in this analysis) resulted in a more severe violation of the assumptions of the repeatability model. Records on the first test day which tend to have low estimates of heritability and low genetic correlation with the tenth test day records may be excluded without much drop in the accuracy of prediction. Predicting lactation

performance from successive test day records in first lactation, Pander and Hill (1993) concluded that there was very little loss in accuracy when the first test day record was excluded from an index based on the first five test day records. Similarly, there was little increase in accuracy of an index of all 10 test day records when the last 2 to 3 test day records were considered. The genetic correlations between successive test days taken in mid-lactation were close to unity and their heritability estimates did not differ much (Chapter 2). Therefore, fewer successive test day records, especially those taken in mid-lactation (i.e. test days 4 to 7), could be considered ignoring the early and later test day records in the genetic prediction of lactation performance assuming a repeatability model. Alternatively, to use all successive test day records, those of similar heritabilities and with high genetic correlations between them could be grouped together as one trait, e.g. as partial yields during lactation (see Chapter 5). Such groupings of test day records as traits could then be used in a repeatability model. Otherwise, a multivariate model might be best for handling all successive test day records.

Chapter 5

Relationship between test day yields and persistency

5.1 Introduction

Persistency of milk yield during lactation provides a convenient means of describing the lactation curve. Grossman, Kuck and Norton (1986) indicated that the same amount of milk can be produced by different lactation curves; and they defined persistency in relation to the flatness of the lactation curve for a given amount of production. Cows that produce moderately with high persistency throughout lactation usually will be under less stress than cows that are less persistent and have a large differential between production at peak and at end of lactation. Persistency as a trait has an economic importance in the management of dairy cows as a flat lactation curve facilitates feeding of cows according to their requirements. This avoids metabolic disorders and possible health problems caused by the physiological strain put on cows with high peak yields (Sölkner and Fuchs, 1987; Swalve, 1994b). Therefore, a moderate initial yield combined with high persistency of lactation is preferrable to high initial yield combined with rapid decline in yield.

Despite its economic importance, persistency of production is ignored in genetic evaluations of dairy cows and sires. In describing the persistency of milk production during lactation, the choice of a parameter that gives a correct description of the shape of lactation curve is important. The lactation curve can be described either by ratios between parts of the lactation or by using a more complicated non-linear mathematical functions as those developed by Wood (1967).

Arbitrarily, a complete lactation may be divided into three parts of about 100 days each and the ratios between the production in these stages of lactation provide a measure of persistency, which describes the variation or lack of it between partial yields during lactation. This approach can also be used to study the variation between test day yields during the second and third 100 days relative to the first 100 days of lactation. Describing the persistency as a variation is, in fact, a logical method but until recently, it was seldomly considered. The ratio measures, which give the relative proportions of yield in different stages of lactation, were introduced by Johansson and Hansson (1940); and have been widely used and found to be appropriate in measuring persistency (Madsen, 1975; Schneeberger, 1981; Danell, 1982b; Sölkner and Fuchs, 1987; Swalve, 1994b).

Linear regressions of milk yield on stage of lactation have also been used to give a measure of persistency (Gravert and Baptist; 1976). More recently, Ptak and Schaeffer (1993) described test day models that incorporate regression coefficients on various functions of days in milk to account for the effect of both the stage of lactation and shape of the lactation curve on production. Schaeffer and Dekkers (1994) suggested that the shape of the lactation curve can be viewed as two sets of

regressions of days in milk. The first set is common to all cows and could be considered as phenotypic in nature. The second set of regression coefficients peculiar to each cow would be random variables because of their association with random animal effects. Schaeffer and Dekkers (1994) concluded that random regressions would allow for genetic differences in the persistency and traits associated with the shape of lactation curves of cows.

The aim of the study was to use the relative proportions of milk yield in successive stages of lactation to provide ratio measures of persistency of milk production. The genetic relationships of persistency with partial milk yields derived from test day yields were then examined.

5.2 Material and Methods

From the test day records on 24435 cows in their second lactation, the partial yields for first, second and third 100 days of lactation were calculated as linear combinations of test day yields representing the different parts of the lactation as follows:

PY_1, the partial yield for the first 100 days as partial yield of test days 1 to 4;

PY_2, the partial yield for the second 100 days as partial yield of test days 5 to 7;

PY_3, the partial yield for the third 100 days as partial yield of test days 8 to 10.

The total lactation yield was computed using a linear interpolation method from 10 monthly test day records according to Milk Marketing Board's Method 3 formula. For details see Chapter 2.

The persistency measures, $P_{2:1}$ and $P_{3:1}$, were calculated from these partial yields as PY_2 divided by PY_1 and as PY_3 divided by PY_1 respectively and expressing them as percentages. These represent ratios between, approximately, the partial milk yields of the second and third 100 days of lactation, respectively and that of the first 100 days. The persistency measures $P_{2:1}$ and $P_{3:1}$ follow a normal distribution. However, being ratios where both the numerators and the denominators can vary, the statistical properties of these persistency measures are not the best (Danell, 1982b). The expected variance of the ratio may be given by the the following approximation (Mood, Graybill and Boes; 1974):

$$var\left(\frac{x}{y}\right) \approx \left(\frac{E(x)}{E(y)}\right)^2 \left(\frac{var(x)}{[E(x)]^2} + \frac{var(y)}{[E(y)]^2} - 2\frac{cov(x,y)}{E(x)E(y)}\right) \tag{5.1}$$

where $E(x) = \mu_x$ and $E(y) = \mu_y$; and x representing either PY_2 or PY_3 for $P_{2:1}$ or $P_{3:1}$ respectively while y represents PY_1 for both ratio measures.

A multi-trait sire model was used in the analysis to estimate the variance-covariance components for the persistency measures and partial and lactation milk yields using REMLPK programs. The statistical model for the analysis was the same as that considered for the multivariate analysis of individual test day yields (see Chapter 2).

Table 5–1: Phenotypic means of partial yields of milk and ratio measures of persistency (per cent) for cows in their second lactation ($n = 24345$).

Trait	Mean	SD.
Lactation milk yield (kg)	6078	1113
Partial milk yields (kg)		
PY_1	97.8	17.76
PY_2	57.6	12.45
PY_3	43.1	11.33
Persistency measure ($\times$ 100)		
$P_{2:1}$	59.12	8.51
$P_{3:1}$	44.48	10.53

5.3 Results

Means and standard deviations for ratio measures of persistency and the partial and lactation milk yields are given in Table 5–1. The estimates of heritability of the ratio measures of persistency and partial and total lactation milk yields and the correlations between them are presented in Table 5–2. The partial milk yields all had high heritability estimates, particularly for PY_2 which was similar to the estimate for lactation milk yield. Estimates of genetic correlation between the ratio measures of persistency and the partial yields during the second and

third 100 days of lactation were all high and positive (0.81–0.90), but were not as high with total yield (0.74 and 0.63). The genetic correlations between the partial yield during peak production (PY_1) and persistency measures were much lower — 0.42 and 0.29 for $P_{2:1}$ and $P_{3:1}$ respectively. Among the partial yields, the genetic correlations were higher between PY_1 and PY_2 (0.85) and between PY_2 and PY_3 (0.88) than between PY_1 and PY_3 (0.68). The partial yield in mid-lactation (PY_2) had got the highest correlation and near unity of 0.98 with total lactation yield. Estimates of phenotypic correlation between PY_1 and persistency measures, $P_{2:1}$ and $P_{3:1}$ were negative and low (-0.08 and -0.15 respectively). Generally, the phenotyic correlations between yields and persistency were lower than the genetic correlations.

5.4 Discussion

By definition of the ratio measures, high absolute values stand for good persistency. $P_{2:1}$ was slightly higher than $P_{3:1}$ indicating that the decrease in milk yield relative to the level of yield in early lactation was greater during the last 105 days of lactation than it was in the second 100 days. This follows from the magnitudes of the partial yields during these different parts of lactation. Persistency measured as ratios between milk yields for different stages during lactation were lower than those values reported by Madsen (1975) and Sölkner and Fuchs (1987) for $P_{2:1}$ and $P_{3:1}$. Even though the persistency measures were based on ratios of different stages of lactation, the partitioning of the lactation into three parts was arbitrary

Table 5–2: Genetic (below diagonal) and phenotypic (above diagonal) correlations between different persistency measures and partial and lactation milk yields with their heritability estimates (diagonal).

	$P_{2:1}$	$P_{3:1}$	PY_1	PY_2	PY_3	LMY
$P_{2:1}$	**0.29**	0.54	-0.08	0.61	0.44	0.33
$P_{3:1}$	0.75	**0.30**	-0.15	0.26	0.80	0.30
PY_1	0.42	0.29	**0.35**	0.72	0.44	0.87
PY_2	0.83	0.81	0.85	**0.50**	0.66	0.91
PY_3	0.85	0.90	0.68	0.88	**0.47**	0.78
LMY	0.74	0.63	0.91	0.98	0.90	**0.51**

as the cumulative yields were calculated from monthly test day yields and not from actual daily yields. Any division of lactation into stages should be based on a more natural partitioning of total lactation yield to represent rising and declining parts. Among the partial yields, the yield during the second part has the highest estimate of heritability. This part of the lactation is made up of test day yields taken during mid-lactation which have got high heritability estimates. The heritability for the partial yield during the last third of lactation was higher than for that for the yield during the first 100 days or so of lactation. Heritability estimates for partial milk yields followed similar trends to those obtained for individual test day yields (see Chapter 2) as the genetic and phenotypic correlations among component test day records were similar. Moreover, the expected variance for each partial yield was equal to the sum of the variances of each component test day yield plus twice the sum of all possible covariances.

The estimates of heritability for the persistency measures were moderate and are within the range of values reported in the literature. Madsen (1975) obtained heritability estimates as high as 0.59 and 0.47 for $P_{2:1}$ and $P_{3:1}$ respectively for first lactation records. Schneeberger (1981) reported heritabilities of 0.22 for $P_{2:1}$ and 0.29 for $P_{3:1}$. Sölkner and Fuchs (1987) found heritabilities of 0.13 and 0.20 for $P_{2:1}$ and $P_{3:1}$ respectively when estimates were pooled for the first three lactations. These results indicate that persistency measures that include the last third 100 days of lactation are more heritable. In this study, the two ratio measures of persistency had heritability estimates of almost the same magnitude.

Partial yield of milk production taken during the second 100 days of lactation

was highly correlated to lactation yield. This is in agreement with results of Danell (1982b), Sölkner and Fuchs (1987) and, more recently, Swalve (1994); and suggests that test day yields taken during mid-lactation can be used to predict lactation yield. These estimates of genetic correlations give an indication of the expected change in yield when selection is based on a different persistency measure with reference to a particular stage of lactation. Peak yield or early lactation yield had a negative phenotypic correlation and low genetic correlation with both persistency measures; and this is an indication that a good persistency measure should have no positive effect on peak yields. The high genetic correlations between lactation milk yield and persistency also indicate that persistency of production can be improved by selecting for lactation yield.

Chapter 6

Summary and General Conclusions

For the genetic analysis of test day records, herd-year-month of first test was found to be the most important main fixed effect, accounting for a higher proportion of the variation for any environmental effect specific to the time of test. Considering this effect in a multivariate model for genetic analysis of test day records as individual traits gave high estimates of genetic parameters due to a relatively increased sire and reduced residual components of variance. These estimates, however, had high standard errors because of the very low average number of effective records per sire. In another model, when herd-year-season of first test was considered as the main effect, the number of subclasses of the main fixed effect was reduced. This improved the data structure, as there was an increase in the average number of effective records per sire from the available records used in the analysis. For the multivariate genetic analysis of test day records, the model fitting herd-year-season of first test as the main fixed effect was used because it improved the data structure and distribution of the effective records from available records. This had the same effect as herd-year-month of first test in accounting for more variation

in test day yield, especially as lactation progressed, with a significant reduction in the residual variances. However, in future analyses with a larger data set, herd-year-month of first test should be considered as the main fixed effect to account for the environmental variation specific to the period of test.

The analysis of single test day records showed that the heritability of yield during the lactation was lowest in the early lactation and increasing during mid-lactation. Records taken on the first test appeared erratic because the unexplained part of the total variance tend to be highest. The estimates of genetic correlations between test day records and complete lactation record for any milk trait were also highest in mid-lactation; and the genetic correlations among test day records were highest for adjacent test days. The phenotypic correlations were lower than the corresponding genetic correlations, but both followed the same pattern. Generally, these genetic parameters would be used in any multivariate evaluation on the basis of test day records as different traits. Prediction of lactation performance from test day yields is a function of their heritabilities and their genetic correlation with 305-day yield. Therefore, it may not be sufficiently accurate to predict the complete lactation from the earliest tests (particularly test day 1 records) as they had low heritabilities and their genetic correlations with complete lactation were also less than 0.90. But the high heritabilities of test day yields and their high genetic correlations with 305-day lactation yields during mid-lactation indicate that the mid-lactation test day records may be used to predict the complete lactation performance. Phenotypic selection indices could be developed from these genetic parameters (i.e. using the mid-lactation estimates) for the prediction of total yield for second lactation in a manner suggested by Pander and Hill (1993)

without much loss in accuracy. Evaluation could thus be carried out on the basis of such predictions using test day records and selection decisions made much earlier in the production life of a cow. Therefore, the potential loss in accuracy of the indirect selection of lactation performance based on mid-lactation test day records might be compensated by reduced generation interval.

Variance components for test day yields in multiple lactations were estimated using a bivariate model. In this analysis, one year's records were considered so that cows had records in only one lactation. Given the correct fixed effect model, the statistical procedure of Schaeffer *et al.* (1978) for the estimation of genetic variance components for a test day yield trait between pairs of lactations, in a basically bivariate analysis is appropriate. In this procedure, yields in any two lactations are considered as separate traits on different cows with zero error covariances between them. For reasonable estimates of genetic parameters, it is important to use a model which accounts for selection bias. If selection is assumed to be carried out across the main effects in multiple lactations, the multi-trait mixed model procedure of Henderson (1975a) would remove any such bias due to selection. The main source of bias in the model used seemed to be due to the effect of proven sires which contributed to the estimation of sire variance components which is not removed by having data on different cows in all lactations. This caused a downward bias in the estimates of random genetic effects. Therefore, in any model of analysis, the most widely used proven sires should be considered fixed so that their daughters' records would contribute to only the within- and not the between-sire components of variance. For analysis of test day records in multiple lactations, the bivariate procedure, whereby test day yields in any two lactations

are considered as separate traits on different cows with zero error covariances between them, is expected to yield unbiased estimates of genetic parameters for test day yields between pairs of lactations. In this analysis, the heritability estimates were heavily biased due to all sires being considered random and unrelated. However, the high genetic correlations between adjacent lactations, especially for test day 5 yields indicate that mid-lactation test day yields in all three lactations could be regarded as the same trait. This implies that the sire ranking was the same for mid-lactation test day yields in all lactations irrespective of age of cows. The genetic correlations between first and second lactations and between second and third lactations for all the traits were high; this indicates that phenotypic indices developed for the prediction of lactation yield on the basis of test day multivariate parameter estimates for the first lactation could be applied for the second lactation and, similarly, for the third lactation.

The use of a repeatability model for analysing test day records may underestimate parameters due to the violation of assumptions implied in a repeated-record animal model; i.e., the genetic correlation between consecutive records is near unity with equal heritabilities for all traits. The analysis of test day yields as repeated records may, therefore, be considered multivariate since there is departure from uniformity of the variance-covariance structure. As test day records are the actual measurements taken on cows, the most accurate method for genetic evalution would be multivariate best linear unbiased prediction (BLUP) based directly on test day records. However, if computational aspects call for a reduction in the number of test day records used per cow, then only those test day records taken in mid-lactation should be considered ignoring those at the beginning and at the end

of the lactation. Therefore, for the analysis of test day yields under a repeatability model, it may be appropriate to consider the use of a few test day records (i.e. test days 4 to 7) taken at mid-lactation with the intuitive assumption that heritabilities are equal and the genetic correlation among all pairs of records is near unity. With this approach, genetic prediction of lactation performance from test day records can be implemented assuming a repeatability animal model especially when considering records in progress and incomplete lactations.

Persistency of milk production may be expressed in terms of ratios based on partial yield variations derived from test day yields during different stages of lactation. The estimates for heritability for these ratio measures of persistency were found to be moderate. The genetic relationship between persistency and partial yields indicated that the partial yields of milk production during the second 100 days of lactation was highly correlated to lactation yield. The high positive genetic correlation between milk yield and persistency was also an indication that selection for milk yield would also ensure that persistency is increased. It might be possible to include persistency into an index with yield in order to achieve improvement in overall yield and persistency. In view of the high genetic correlations among the partial yields, such groupings calculated as linear combinations of test day yields representing successive stages of lactation could be used in a repeatability model as a better alternative to using all individual test day records. Peak yield or early lactation yield had a negative phenotypic correlation with both ratio measures of persistency, an indication that a high level of production had a negative influence on variation. In general, any useful measure of persistency should exhibit an appreciable amount of genetic variability as indicated by moder-

of the lactation. Therefore, for the analysis of test day yields under a repeatability model, it may be appropriate to consider the use of a few test day records (i.e. test days 4 to 7) taken at mid-lactation with the intuitive assumption that heritabilities are equal and the genetic correlation among all pairs of records is near unity. With this approach, genetic prediction of lactation performance from test day records can be implemented assuming a repeatability animal model especially when considering records in progress and incomplete lactations.

Persistency of milk production may be expressed in terms of ratios based on partial yield variations derived from test day yields during different stages of lactation. The estimates of heritability for these ratio measures of persistency were found to be moderate. The genetic relationship between persistency and partial yields indicated that the partial yields of milk production during the second 100 days of lactation was highly correlated to lactation yield. The high positive genetic correlation between milk yield and persistency was also an indication that selection for milk yield would also ensure that persistency is increased. It might be possible to include persistency into an index with yield in order to achieve improvement in overall yield and persistency. In view of the high genetic correlations among the partial yields, such groupings calculated as linear combinations of test day yields representing successive stages of lactation could be used in a repeatability model as a better alternative to using all individual test day records. Peak yield or early lactation yield had a negative phenotypic correlation with both ratio measures of persistency, an indication that a high level of production had a negative influence on variation. In general, any useful measure of persistency should exhibit an appreciable amount of genetic variability as indicated by moder-

ate to high heritability. The ratios based on partial yield variations thus provide a good measure of persistency. Further studies should be conducted to identify the different stages of lactation, particularly using daily milk yields to obtain a more natural partitions of total yield during lactation. There is also a need to examine the relationships between persistency and partial yields derived from test day fat and protein yields with the aim of developing selection indices for milk production that incorporate yields of milk components during successive stages of lactation and their persistency.

From the results obtained in these studies, the genetic prediction of total lactation yield from test day records could be based on mid-lactation records without much loss in accuracy. In constructing selection indices based on single test day records for the genetic prediction of total lactation, the first test day may not be considered. Records taken on the first test tend to be erratic and also have low heritability estimates because the unexplained part of the total variance is highest. Several workers (Danell, 1982a; Wilmink, 1987; Swalve, 1995) have warned against too much consideration of the first test day record for selection decisions. The procedure outlined by VanRaden *et al.* (1991) and Pander and Hill (1993) that includes records in progress in the genetic evaluation currently adopted by the Animal Data Centre for the U. K. evaluations based on first lactation records may also be applied in successive lactations. However, the appropriate expansion factors and weights for later lactations, which depend on the lactation length of the record and parity, need to be obtained.

References

Ali, T. E. and Schaeffer, L. R. 1987. Accounting for covariances among test day milk yields in dairy cows. *Canadian Journal of Animal Science* **67**: 637–644.

Anderson, S. M., Mao, I. L and Gill, J. L. 1989. Effect of frequency and spacing of sampling on accuracy and precision of estimating total lactation yield and characteristics of the lactation curve. *Journal of Dairy Science* **72**: 2387–2394.

Animal Data Centre. 1995. UK Statistics for Genetic Evaluations (Dairy). *An ADC Publication, Rickmansworth, England. February, 1995. 110pp*

Barker, J. S. F. and Robertson, A. 1966. Genetic and phenotypic parameters for the first three lactations in Friesian cows. *Animal Production* **8**: 221–240.

British Standards Institution. 1972. Methods for calculating the total quality of milk and butterfat and the average percentage of butterfat. *British Standards No.* 4856 pp 12–17.

Cassell B. G. and McDaniel, B. T. 1983. Use of later records in dairy sire evaluation: A review. *Journal of Dairy Science* **66**: 1–10.

Chauhan, V. P. S. and Hill, W. G. 1986. Seasonal grouping in a herd-year-season model of sire evaluation. *Animal Production* **43**: 63–71.

Danell, B. 1982a. Studies on lactation yield and individual test-day yields of Swedish dairy cows. II. Estimates of genetic and phenotypic parameters. *Acta Agriculturae Scandinavica* **32**: 82–92.

Danell, B. 1982b. Studies on lactation yield and individual test-day yields of Swedish dairy cows. III. Persistency of milk yields and its correlation with milk yield. *Acta Agriculturae Scandinavica* **32**: 93–101.

Danell, B. 1990. Genetic aspects of different parts of lactations. *Proceedings of the 4th World Congress on Genetics Applied to Livestock Production. Edinburgh, Scotland, UK.* Vol. 14 pp 114–117.

Eriksson, J - Å. 1982. Estimating sire's genetic value for milk yield in first and second lactation by different mixed model procedures, using selected second lactation records. *Acta Agriculturae Scandinavica* **32**: 193–206.

Falconer, D. S. 1989. *Introduction to Quantitative Genetics.* Third Edition. Longman, London.

Gravert, W. L. and Baptist, R. 1976. Breeding for persistency of milk yield. *Livestock Production Science* **3**: 27–31.

Grossman, M., Kuck, A. L., Norton, H. W. 1986. Lactation curves of purebred and crossbred cattle. *Journal of Dairy Science* **69**: 195–203.

Henderson, C. R. 1975a. Best linear unbiased estimation and prediction under a selection model. *Biometrics* **32**: 423–447.

Henderson, C. R. 1975b. Comparison of alternative sire evaluation methods . *Journal of Animal Science* **41**: 760–770.

Henderson, C. R. 1990. Accounting for selection and mating biases in genetic evaluations. *Advances in statistical methods for genetic improvement.* D. Gianola and K. Hammond (*Eds.*). Springer-Verlag, Berlin. pp 413–436.

Johansson, I. and Hansson, A. 1940. Causes of variation in milk and butterfat yield in dairy cows. *Kungl. Landtbr. Akad. Tidskr.* **79**: 1–127. (cited by Danell, 1982b).

Jones, L. P. and Goddard, M. E. 1990. Five years experience with animal model for dairy cattle evaluations in Australia. In: it Proceedings of the 4th World Congress on Genetics Applied to Livestock Production. Edinburgh, Scotland, UK. Vol. 13 pp 382–385.

Keown, J. F. and Van Vleck, L. D. 1971. Selection on test day fat percentage and milk production. *Journal of Dairy Science* **54**: 199–203.

Lee, A. J. 1978. Mixed model evaluation of related sires for milk yield eliminating age and interaction of sire with herd-year-season. *Journal of Dairy Science* **61**: 600–606.

Madsen, O. 1975. A comparison of some suggested measures of persistency of milk yield in dairy cows. *Animal Production* **20**: 191–197.

Maijala, K. and Hanna, M. 1974. Reliable phenotypic and genetic parameters in dairy cattle. In: *Proceedings of the 1st World Congress on Genetics Applied to Livestock Production. Madrid, Spain.* Vol. 1 pp 541–563.

Meyer, K. 1984. Estimates of genetic parameters for milk and fat yield for the first three lactations in British Friesian cows. *Animal Production* **38**: 313–322.

Meyer, K. 1985. Maximum likelihood estimation of variance components for a multivariate mixed model with equal design matrices. *Biometrics* **41**: 153–165.

Meyer, K. 1986. Restricted maximum likelihood to estimate genetic parameters — In Practice. *Proceedings of the 3rd World Congress Genetics Applied to Livestock Production, Lincoln, Nebraska, USA.* Vol. 12 pp 454–459.

Meyer, K. 1987. Estimates of variance due to sire x herd interaction and environmental covariances between paternal half-sibs for first lactation dairy production. *Livestock Production Science* **17**: 95–115.

Meyer, K. 1991. DFREML — Programs to estimate variance components by Restricted Maximum Likelihood using a Derivative - Free Algorithm. *Users' Notes. Animal Genetics and Breeding Unit, University of New England, Armidale, New South Wales, Australia.* 84pp.

Meyer, K., Graser, H-U. and Hammond, K. 1989. Estimates of parameters for first lactation test day production of Australian Black and White cows. *Livestock Production Science* **21**: 177–199.

Mood, A. M., Graybill, F. A. and Boes, D. C. 1974. *Introduction to the Theory of Statistics.* Third Edition. McGraw-Hill.

Nicholson, H. H., Schaeffer, L. R., Burnside, E. B. and Freeman, M. G. 1978. Use of later records in dairy sire evaluation. *Canadian Journal of Animal Science* **58**: 615–620.

Pander, B. L. and Hill, W. G. 1993. Genetic evaluation of lactation yield from test day records on incomplete lactation. *Livestock Production Science* **37**: 23–36.

Pander, B. L., Hill, W. G. and Thompson, R. 1992. Genetic parameters of test day records of British Holstein-Friesian heifers. *Animal Production* **55**: 11–22.

Pander, B. L., Thompson, R. and Hill, W. G. 1993. The effect of increasing the interval between recordings on genetic parameters of test day yields of British Holstein-Friesian heifers. *Animal Production* **56**: 159–164.

Patterson, H. D. and Thompson, R. 1971. Recovery of interblock information when block sizes are unequal. *Biometrika* **58**: 545–554.

Ptak, E. and Schaeffer, L. R. 1993. Use of test day yields for genetic evaluation of dairy sires and cows. *Livestock Production Science* **34**: 23–34.

Rothschild, M. F., Henderson, C. R. and Quaas, R. L. 1979. Effects of selection on variances and covariances of simulated first and second lactations. *Journal of Dairy Science* **62**: 996–1002.

Schaeffer, L. R. and Dekkers, J. C. M. 1994. Random regressions in animal models for test day production in dairy cattle. *Proceedings of the 5th World Congress on Genetics Applied to Livestock Production. Guelph, Canada.* Vol. 18. pp 443–446.

Schaeffer, L.R., Wilton, J.W. and Thompson, R. 1978. Simultaneous estimation of variance and covariance components from multitrait mixed model equations. *Biometrics* **34**: 199–208.

Schneeberger, M. 1981. Inheritance of lactation curve in Swiss Brown cattle. *Journal of Dairy Science* **64**: 475–483.

Simianer, H. 1986. A general approach to the use of multiple traits with repeated measurements in the estimation of breeding values. *Livestock Production Science* **15**: 315–324.

Sölkner, J. and Fuchs, W. 1987. A comparison of different measures of persistency with special respect to variation of test-day milk yields. *Livestock Production Science* **16**: 305–319.

Strandberg, E. 1990. Value of later lactations in dairy cattle breeding. *Proceedings of the 4th World Congress on Genetics Applied to Livestock Production, Edinburgh, Scotland, UK.* Vol. 14 pp 5–14.

Swalve, H. H. 1994. Genetic relationships between testday milk production and persistency in dairy cattle performance records. *Proceedings of the 5th World Congress on Genetics Applied to Livestock Production. Guelph, Canada.* Vol.18. pp 467–470.

Swalve, H. H. 1995. The effect of test day models on the estimation of genetic parameters and breeding values for dairy yield traits. *Journal of Dairy Science* **78**: 929–938.

Thompson, R. 1977. Estimation of quantitative genetic parameters. *Proceedings of International Conference on Quantitative Genetics.* E. Pollak, O. Kempthorne and T. B. Bailey (*Eds*). Iowa State University Press, Ames. pp 639–657.

Thompson, R. and Hill, W. G. 1990. Univariate REML analysis for multivariate data with the animal model. *Proceedings of the 4th World Congress on Genetics Applied to Livestock Production, Edinburgh, Scotland, UK.* Vol. 13 pp 484–487.

Thompson, R. and Meyer, K. 1986. A review of theoretical aspects in the estimation of breeding values for multi-trait selection. *Livestock Production Science* **15**: 299–313.

Tong, A. K. W., Kennedy, B. W. and Moxley, J. E. 1979. Heritabilities and genetic correlations for the first three lactations from records subject to culling. *Journal of Dairy Science* **62**: 1784–1790.

Trus, D. and Buttazzoni, L. G. 1990. A multitrait approach to modelling the lactation curve. In: *Proceedings of the 4th World Congress on Genetics Applied to Livestock Production, Edinburgh, Scotland, UK.* Vol. 13 pp 492–495.

Van der Werf, J. H. J. and De Boer, W. 1989. Influence of nonadditive effects on estimation of genetic parameters in dairy cattle. *Journal of Dairy Science* **72**: 2606–2614.

VanRaden, P. M., Wiggans, G. R. and Ernst, C. A. 1991. Expansion of projected lactation yield to stabilize genetic variance. *Journal of Dairy Science* **74**: 4344–4349.

Van Vleck, L. D. 1985. Including records of daughters of selected bulls in estimation of sire components of variance. *Journal of Dairy Science* **68**: 2396–2402.

Van Vleck, L. D. and Gregory, K. E. 1992. Differences in heritability estimates from multi-trait and repeated-records models. *Journal of Animal Science* **70**: 2994–2998.

Visscher, P. M. and Thompson, R. 1992. Univariate and multivariate parameter estimates for milk production traits using an animal model. I. Description and results of REML analyses. *Genetics, Selection, Evolution* **24**: 415–430.

Weller, J. I. 1988. Inclusion of partial lactations in genetic analysis of yield traits by differential weighting of records. *Journal of Dairy Science* **71**: 1873–1879.

Wickham, B. W. and Henderson, C. R. 1977. Sire evaluation by second lactation records of daughters. *Journal of Dairy Science* **60**: 96–107.

Wiggans, G. R. and Van Vleck, L. D. 1979. Extending partial lactation milk and fat records with a function of last sample production. *Journal of Dairy Science* **62**: 316–325.

Wiggans, G. R., Misztal, I. and Van Vleck, L. D. 1988. Implementation of an animal model for genetic evaluation of dairy cattle in the United States. *Journal of Dairy Science* **71** *(Suppl. 2)* : 54–69.

Wilmink, J. B. M. 1987. Efficiency of selection for different cumulative milk, fat and protein yields in first lactation. *Livestock Production Science* **17**: 211–224.

Wilmink, J. B. M. 1988. Effects of incomplete records on genetic parameters among cumulative yields in first lactation and on extension of part lactations. *Livestock Production Science* **18**: 19–34.

Wood, P. D. P. 1967. Algebraic model of the lactation curve in cattle. *Nature* **216**: 164–165.